THE PALATINE-MAXILLARY MECHANISM IN CATFISHES, WITH COMMENTS ON THE EVOLUTION AND ZOOGEOGRAPHY OF MODERN SILUROIDS

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ABSTRACT: The mechanism used by catfishes for ex-
tending the maxillary and its barbel was studied in
various groups. The objective was to determine the
probable structural pathways that have led to the
different representations of this mechanism among
modern siluroids.

Preliminary discussions deal with the identity
of certain bones in the catfish suspensorium,
notably the ectopterygoid and mesopterygoid, and
with the mechanics of the palatine-maxillary system.

The results of the study have been interpreted
as follows. The palatine-maxillary mechanism is
represented in modern catfishes by two basal types:
that of *Diplomystes* with a toothed maxillary, and
that of the Bagridae, Ariidae, and several other
families in which the mesopterygoid forms a movable
link between the palatine and the posterior part
of the suspensorium. The amblycipitids have a

suspensorial structure that may represent an early
deviation from the type found in the Bagridae, but
all other catfishes investigated have palatine-
maxillary mechanisms which, so far as structure is
concerned, could apparently have been derived from
the sort represented in the Bagridae. A direction
of specialization that has been developed frequently
and in various ways is that found in such hill-
stream families as the Trichomycteridae, Amphiliidae,
and Sisoridae. Other directions of specialization
have been followed by the Chacidae, Plotosidae,
Mochokidae, and Siluridae, with the palatine-
maxillary mechanism of *Silurus* perhaps the most
divergent from the basal bagrid type of all of the
catfishes investigated.

The implications of these results have been
extrapolated into a set of working hypotheses con-
cerning catfish evolution and zoogeography. It is
hypothesized that primary adaptive radiations from
a basal pimelodid-bagrid stock have occurred in
South America and Asia, with Africa an important
but secondary center of diversification.

INTRODUCTION

All catfishes have a palatine-maxillary mechanism
(Eaton, 1948; Alexander, 1965) that extends the maxillary
and its barbel, but no other group shows this specialization.
A knowledge of the nature and variation of this mechanism
may contribute toward our understanding of the inter-
relationships of catfishes, a subject upon which records of
fossil siluroids as yet throw little light (Lundberg & Case,
1970).

Modern catfishes are the endpoints of a tremendous
adaptive radiation (Rossi, 1951), represented by some 2000
species (Bailey, 1971) allocated to about 31 families
(Greenwood, *et al.*, 1966; Gosline, 1971). With regard to
family classification Tilak (1967b, p. 288) quotes Gar-
stang's comment about a "proliferation of pigeonholes."
However, Alexander ends his 1965 paper with the statement:
"So much parallel evolution has occurred within the catfish
that any attempt to reconstruct the phylogeny of the sub-
order would seem, in the present state of our knowledge,
unprofitable."

One approach to the unraveling of siluroid phylogeny is
the intensive and extensive investigation of particular
structures or structural systems. Units that have been
previously studied in a more or less wide range of catfishes
are the caudal skeleton (Lundberg & Baskin, 1969), the
pelvic girdle (Shelden, 1937; Tilak, 1968), the pectoral
girdle (Tilak, 1963b), the Weberian apparatus and associated
structures (Bridge & Haddon, 1893; Chranilov, 1929; Chardon,
1968), and the otoliths (Frost, 1925; Tilak, 1964b).

The present paper deals with the palatine-maxillary
mechanism.   Inasmuch as this is functionally associated with
feeding, it is perhaps especially subject to the parallel
changes inherent in adaptive radiation.   However, the
classification of catfishes has always been more or less
heavily based on attributes associated with the mechanism,
e.g., the maxillary teeth of *Diplomystes*.   It seems, there-
fore, high time that the nature of the variation in the
palatine-maxillary mechanism in catfishes be accorded more
attention than it has hitherto received.

Several levels of structural organization in the
palatine-maxillary mechanism seem recognizable among modern
catfish groups.   Sometimes it is possible to follow in
detail the structural transitions from one level to the next.
But unless different catfish groups followed demonstrably
different morphological pathways it is impossible to dis-
tinguish between parallel lines of change.   In the palatine-
maxillary mechanism it seems that certain potentialities for
structural evolution have been followed out repeatedly and,
so far as I can determine, over essentially similar pathways.
Thus, though it seems "unprofitable" to attempt any "phy-
logeny" of palatine-maxillary mechanisms, the information
to be presented below does bear rather decisively on certain
aspects of catfish evolution.

METHODS

The palatine-maxillary mechanism and structures
associated with it consist of bone, cartilage, ligamentous
tissue, and muscle that are not easily studied without
dissection.   In the present investigation, alcohol-preserved
specimens provided the primary material.   Two dissections
starting from different points were usually made.   In one,
the lacrimal was folded back, the eyeball and cheek muscles
were often moved out of the way, and material lateral to the
palatine was cleaned off.   In the other, the skin of the
roof of the mouth was removed through the mouth opening.
Prepared skeletons and cleared and stained specimens were
examined, but both of these types of material present
difficulties in the observation of cartilage, musculature,
and ligamentous tissue.

BONE NAMES.   There are two somewhat different problems
concerning bone names in catfishes: one nomenclatural, the
other zoological.   The zoological problem has to do with
the identification of certain bones and will be dealt with
at the proper points in the text.   Nomenclaturally,
mesopterygoid will here be used for the bone often called
endopterygoid, and ectopterygoid for that called pterygoid.
In catfishes there appears to be no true dermopalatine; the
palatine component of the palatine-maxillary mechanism is
therefore an autopalatine.

FISH NAMES. No reclassification is suggested in this
paper, which deals with a single suite of structures and not
with whole fishes. The classification adopted is merely one
that seems reasonable and intelligible. Except for
Diplomystes, no attempt has been made to solve nomenclatural
problems regarding family or other names. No effort has
been made to check the identifications on the specimen
labels.

The Cypriniformes (= the ostariophysine fishes) is con-
sidered as a single order made up of two suborders:
Siluroidei (the catfishes) and Cyprinoidei (the characins,
gymnotids, cyprinids, and their allies). The classification
of catfish families is basically that of Regan (1911). The
Doradidae as here understood includes the Auchenipterinae.
The Ariidae is the Tachysuridae of authors. The classifi-
cation of the Bagridae is that of Jayaram (1966). The
Amblycipitidae comprises the genera *Amblyceps* and *Liobagrus*.
The Ictaluridae is the Ameiuridae or Amiuridae of authors,
and the Trichomycteridae is the Pygidiidae. *Nematogenys* is
here included in the Trichomycteridae, and the Bunocephalinae
in the Aspredinidae (Myers, 1960).

MATERIAL USED FOR MORE THAN SUPERFICIAL EXAMINATION. In
the following list of specimens, California Academy of
Sciences material is listed with CAS preceding the catalog
number. All other catalog numbers refer to fishes in the
collections of the University of Michigan Museum of Zoology.

Diplomystidae: *Diplomyste pappilosus*, Santiago market,
    Chile, CAS 13706. (The correct spelling of this generic
    name is apparently *Diplomystes*, Bleeker's latinization
    of Dumeril's French Diplomyste.)
Ariidae: *Arius felis*, Florida, 135912; *A. melanopus*, Guate-
    mala, 143459.
Doradidae: *Trachelyopterus coriaceus*, Bolivia, 66321;
    Hassar lipophthalmus, Colombia, 185333.
Bagridae: *Chrysichthys auratus*, Egypt, 169013; *Auchenoglanis
    ballayi*, Cameroun, 191667; *Bagrus docmac*, Uganda, 187332;
    Bagroides melapterus, Sumatra, 155695; *Rita rita*, Bang-
    ladesh, 187880; *Mystus nemurus*, Thailand, 186784.
Pangasiidae: *Pangasias macronema*, Thailand, 186707.
Schilbeidae: *Schilbe mystus*, Zambia, 189126.
Clariidae: *Clarias batrachus*, Florida, 190122.
Plotosidae: *Plotosus arab*, Madagascar, 185445.
Chacidae: *Chaca chaca*, Bangladesh, 189645.
Sisoridae: *Bagarius bagarius*, Sumatra, 155701.
Siluridae: *Parasilurus asotus*, Japan, 180201.
Amphiliidae: *Amphilius platychir*, Zambia, material on loan
    from the Royal Ontario Museum.
Mochokidae: *Synodontis nebulosus*, Zambia, 189140.
Ictaluridae: *Ictalurus punctatus*, Mexico, 192471; *Noturus
    flavus*, Michigan, 56575.
Pimelodidae: *Pimelodus clarias*, Brazil, 147401; *Rhamdia
    guatemalensis*, Guatemala, 188074; *Pseudopimelodus zungaro*,
    Bolivia, 66312.

Trichomycteridae: *Nematogenys inermis*, Santiago market,
    Chile, CAS 12692; *Trichomycterus rivulatus*, Peru,
    185311.
Aspredinidae: *Aspredinichthys filamentosus*, Georgetown
    market, British Guiana, CAS 16201.

STRUCTURE AND MECHANICS OF THE PALATINE-MAXILLARY SYSTEM

Nasal, mental, and maxillary barbels are variously
developed in catfishes, but only that on the maxillary is
constant.   These barbels can usually be moved by muscles
extending into their bases (Singh, 1967), but the palatine-
maxillary mechanism provides another source of movement for
the maxillary barbel.   This mechanism has two bony parts
derived from different structural systems.   The siluroid
palatine, more precisely autopalatine, is an endochondral
mandibular-arch component of the teleostean suspensorium;
the maxillary, an upper jaw element in lower teleosts, is
ultimately derived from the dermal skull roof of early
actinopterygians (Gregory, 1933).   Most of the evolution of
the maxillary part of the mechanism can apparently be
followed among living catfishes.   The development of its
palatine part, however, seems to have been made possible by
earlier changes in suspensorial structure that require some
discussion.

In most lower teleosts, as in *Elops* (Ridewood, 1904, fig.
10), the suspensorium is a single firmly-knit structural
unit of composite origin, made up partly of endochondral
ossifications and partly of dermal supporting elements.
This suspensorium has movable abutments against the skull at
its anterior (palatine) and posterior (hyomandibular) ends.
Thus the mandible in such fishes is propped away from the
skull mostly by the hyomandibular but partly by the auto-
palatine.   In catfishes, which in this respect appear to
represent an endpoint in an evolutionary trend already pre-
sent in ancestral cypriniform fishes (Gosline, 1973), most
of the dermal elements seem to have 'come loose' from the
suspensorium, and the endochondral ossifications are in two
sections that are, at most, ligamentously interconnected.
Anteriorly, the autopalatine has become a part of the
palatine-maxillary mechanism.   Posteriorly, the hyomandi-
bular-quadrate region has taken over the whole propping
function for the mandible.   The mesopterygoid-ectopterygoid
area, which in most lower teleosts forms a firm strut bet-
ween the anterior and posterior parts of the suspensorium,
has in catfishes lost this function, and its reduced com-
ponents are variably represented or absent.

The rearrangements in the posterior area of the siluroid
suspensorium may be briefly summarized and dismissed from
further consideration.   So long as the suspensorium had a
long, firm horizontal axis, it was equipped to withstand a
longitudinal pull from the contracting M. adductor mandi-
bulae.   But in catfishes this horizontal suspensorial axis

has been fragmented. Probably in association with this
fragmentation, the main axis of contraction of the M.
adductor mandibulae in catfishes has shifted to a more
vertical plane (compare Takahasi, 1925, figs. 1-10; or the
insertions of the M. adductor mandibulae in Alexander's,
1965, fig. 7).

In connection with the closer alignment between the M.
adductor mandibulae and the hyomandibular-quadrate axis of
the suspensorium, that axis has been simplified and pre-
sumably strengthened. The hyomandibular of catfishes has
been brought into direct contact with the quadrate; the
metapterygoid has, so to speak, been extruded forward from
its original position between the anterior part of the
hyomandibular and the quadrate; and posteriorly the
symplectic has disappeared as a separate element. The
preopercle forms a strengthening strut along the posterior
border of the suspensorium. (All of these features are
found again in eels which, like the catfishes, have frag-
mented suspensoria.)

The change toward a closer alignment between the M.
adductor mandibulae and the hyomandibular-quadrate axis of
the suspensorium has also led to certain changes in the
areas of origin and insertion of the muscle (again paralleled
in eels). As to insertion, the coronoid process of the cat-
fish mandible is often low or absent. With regard to origin,
a portion of the M. adductor mandibulae frequently extends,
as in *Diplomystes*, onto the dorsal surface of the cranium.
Whether or not such an extension occurs in catfishes appears
to be associated with mandibular structure. Thus, catfishes
with part of the M. adductor mandibulae originating on the
top of the skull are mostly forms with relatively large,
horizontal mouths, e.g., ictalurids, plotosids, some bagrids.
In catfishes with small mouths, e.g., *Synodontis* (Stix,
1956), the M. adductor mandibulae does not extend over the
cranium. Nor does it extend on to the skull in the large-
mouthed *Silurus*. However, in *Silurus* the lower jaw is
oblique, and fibers of the M. adductor mandibulae are more
horizontally aligned than is usual in catfishes (compare
Takahasi's pl. 1, fig. 8 of *Parasilurus* with pl. 1, fig. 10
of *Plotosus*).

In lower teleosts such as *Elops* (Nybelin, 1968) the
dermal ectopterygoid and mesopterygoid bones have a double
role as tooth-bearing plates and as a structural bridge
between the anterior and posterior parts of the suspensorium.
In characins and cyprinids this bridge is usually represented
as a strut movable at both ends (Gosline, 1973); there are
no teeth on the mesopterygoid, but teeth may be present on
the characin ectopterygoid. In catfishes, these two bones
are not only variable, if present, but the names applied to
them in the literature are so confused that some attempt at
clarification is obligatory.

A true ectopterygoid does not seem to me to be identi-
fiable with certainty in catfishes. Usually in teleosts
the ectopterygoid adjoins the mesopterygoid for much of the

length of both; in catfishes the only bone that ever adjoins
the mesopterygoid is the metapterygoid which, in siluroids,
is forward of its usual position.   In catfishes there is
often, as in *Diplomystes* (Alexander, 1965, fig. 4), a bony
projection extending forward from the lateroventral part of
the metapterygoid; such a projection is usually attached to
the vomerine part of the skull by ligamentous tissue.   Some-
times, as in the bagrid *Rita* or on one side of a skeleton
of the ariid *Arius assimilis* (UMMZ 190074-S), this pro-
jecting area is represented as a separate ossification.
Such an ossification, when it exists, has the position of
the cyprinid ectopterygoid, but it seems to have become
separated from the metapterygoid, which is not a bone the
cyprinid ectopterygoid could have fused with.   To me a more
satisfactory explanation for the ossification under con-
sideration is that it represents a fragmented part of the
metapterygoid.

Often in catfishes there is a tooth-bearing plate on the
oral surface of the ligamentous tissue mentioned above.
Such plates have frequently been identified as ectoptery-
goids, but again the identification seems questionable.
Dentition in the roof of the catfish mouth is very variable.
Teeth are usually present on the premaxillary and often on
the vomer, but they may also be associated with such bones
as the mesethmoid (Starks, 1926, fig. 16) and parasphenoid
(Starks, 1926, fig. 12).   Tooth-bearing plates may also
develop in various areas of the front of the mouth roof
where adjacent structural support is present.   For example,
dental plates may occur just lateral to the premaxillaries
over the ligamentous tissue between the premaxillary and the
lower jaw (Tilak, 1961, fig. 4).   Functionally, such dental
plates provide extensions for the premaxillary band of teeth
just as dental plates on the metapterygoid-vomerine ligament
provide extensions of the vomerine tooth band.   Tooth-bearing
plates on the metapterygoid-vomerine ligament may be separate
from both the vomer and the metapterygoid (Starks, 1926,
figs. 11, 12).   Sometimes such plates may apparently fuse
with the vomer with age (Eigenmann & Eigenmann, 1890, p. 64).
Sometimes part or all of such a tooth plate becomes firmly
attached to the metapterygoid as in the schilbeid *Eutro-
piichthys* (Tilak, 1961, figs. 7, 8) or even fuses with the
metapterygoid as in the bagrid *Chrysichthys auratus* (though
not in the other species of *Chrysichthys* examined).   The
question arises of which, if any, of these tooth plates
represent the usual teleostean ectopterygoid.   (Perhaps the
phrase "ectopterygoid teeth" could usefully be continued as
a regional designation for dentition on the roof of the cat-
fish mouth without prejudice to the question of ectopterygoid
homology.)

Still another element that has been identified as an
ectopterygoid is the small bony ossicle embedded on the
lower surface of the autopalatine of ariids (Starks, 1926,
fig. 11, *p2*; see also Tilak, 1965a, figs. 2, 5) and in the
bagrid *Bagroides* (see below).   Lundberg (*in litt.*) states

that such an ossicle occurs in a cleared and stained speci-
men of *Diplomystes*, but I have been unable to find it in the
unstained fish available to me. In the present paper this
ossicle is provisionally identified as a fragmented part of
the mesopterygoid. A final and different problem arises
from the fact that the (unfragmented) siluroid mesopterygoid
has frequently been misidentified as an ectopterygoid (see
below).

The mesopterygoid is frequently absent in catfishes.
When present it is a toothless bone with a strong antero-
medial ligamentous attachment to the lower surface of the
skull just behind or beside the vomer. (The mesopterygoid
is most easily located by opening the mouth and removing
the skin from the mouth roof.) The catfish mesopterygoid
may extend laterally to below the posterior part of the
autopalatine. When present, it is joined to the metaptery-
goid behind it either directly or by ligament (except in
amblycipitids). Regan (1911) has usually, though by no
means always, identified the mesopterygoid correctly; for
example, he calls the mesopterygoid of pimelodids a pterygoid.
The bone named ectopterygoid in most of Tilak's catfish
papers is the mesopterygoid of the present paper; however,
the entopterygoid of his 1961 work and of figures 2, 7, 9,
and 18 of his 1964(a) paper is the mesopterygoid of this
one. The use of the name mesopterygoid is also confused by
Jayaram (1966).

The basic components of the palatine-maxillary mechanism
are as follows (fig. 1A). There is always a hinge-joint
between the anterior end of the autopalatine (or its carti-
laginous extension) and the posterior face of the median end
of the maxillary. The lateral ethmoid has a flange extending
out to or over the autopalatine, which slides along and/or
rocks around this flange. Movement of the autopalatine is
brought about by contraction of an anterior part of the M.
adductor arcus palatini (Takahasi, 1925). This muscle
originates on the skull and usually inserts along the medial
rim of the posterior part of the autopalatine. There is
generally a nondistensible ligament extending medially from
the anterior face of the median part of the maxillary to the
premaxillary or sometimes (*Synodontis*) to the mesethmoid.
The maxillary rocks around this ligamentous attachment when
autopalatine movement causes lateral or posterior displace-
ment of the palatine-maxillary hinge. The result is to
force the distal end of the maxillary and its barbel forward
(except in plotosids).

Almost all of the palatine components of the siluroid
palatine-maxillary mechanism can be located in one or another
of the cyprinoid fishes (though usually associated with a
different type of maxillary movement). Certain similarities
between the cyprinid palatine and that of *Diplomystes* are
striking. Thus, the cyprinid autopalatine is two-headed
anteriorly, usually with one head extending medially and
articulating with the skull and the other projecting forward
to an abutment against the posterior face of the maxillary.

However, in the cyprinid *Ptychocheilus*, somewhat as in *Diplomystes*, the medial head has moved anteriorly and both heads approach the maxillary.

In cyprinids the posterior part of the palatine has a movable articulation with the mesopterygoid below the lateral flange of the lateral ethmoid, and the M. adductor arcus palatini does not extend forward onto the autopalatine (Takahasi, 1925). In catfishes the posterior end of the autopalatine is free to move in a fore and aft direction; it usually extends well behind the lateral ethmoid flange and is almost always moved directly by a part of the M. adductor arcus palatini that inserts on it. I know of no cyprinoids with the autopalatine free posteriorly. However, in some cobitids, e.g., *Cobitis taenia* and *Misgurnus anguillicaudata*, Takahasi (1925, p. 26) describes the M. adductor arcus palatini as extending forward onto the posterior end of the autopalatine. In the specimen of *Misgurnus fossilis* dissected, the M. adductor arcus palatini does not extend forward quite as far as the autopalatine, but some of its fibers extend almost directly back from the anterior part of the mesopterygoid; contraction presumably pulls the mesopterygoid-autopalatine joint, and hence the autopalatine, backward, thus, but indirectly, having the same effect on the autopalatine as does contraction of the M. adductor arcus palatini in *Diplomystes*.

By way of background to the functioning of the palatine-maxillary system, two matters deserve notice. The first of these is the evolution of muscular coordination in maxillary movement. *Silurus* is said to be able to flutter its maxillary barbels (Juge, 1899). This implies a complete independence between maxillary movements and mouth movements. However, *Silurus*, so far as its palatine-maxillary mechanism is concerned, is one of the most specialized of all catfishes, and its maxillary movements are probably also specialized. The muscular coordination of fishes with more generalized palatine-maxillary mechanisms cannot be determined from preserved specimens, but some circumstantial anatomical evidence is available.

Though the system of retracting the extended maxillary barbel varies greatly from species to species, maxillary retraction in many catfishes appears to be at least partly coordinated with raising of the mandible. This may be brought about by ligamentous tissue of various types between the maxillary and the mandible, as in *Diplomystes* or *Pimelodus* (see below). In many catfishes a maxillary-mandibular ligament is absent, but there is a M. retractor tentaculi. This again may be of various sorts. In *Plotosus* the M. adductor mandibulae serves as a retractor muscle for the maxillary. Here maxillary retraction and raising of the lower jaw are presumably coordinated. Most catfishes with a M. retractor tentaculi have this muscle completely separate from the M. adductor mandibulae. But even here, at least in *Ictalurus*, the M. retractor tentaculi "is supplied by a branch of the same nerve that supplies the deeper

portions of the *add. mand.*" (McMurrich, 1884, p. 314).   It
appears that, whatever independence of movement has been
ultimately attained, retraction of the maxillary and its
barbel in catfishes was originally coordinated with raising
of the mandible, as in teleosts generally.

Extension of the maxillary and its barbel is brought
about in a more uniform manner throughout the siluroids
(except plotosids), i.e., by contraction of the palatine
portion of the M. adductor arcus palatini (Takahasi, 1925;
Stix, 1956).   However, extension of the maxillary in most
catfishes does not seem to be coordinated with mandibular
lowering, as is usual in teleosts, but rather with the
reduction in the size of the oral cavity that results from
contraction of the posterior part of the M. adductor arcus
palatini.   McMurrich (1884), Takahasi (1925) and others have
shown not only that in catfishes the palatine and more
posterior section of the M. adductor arcus palatini are
parts of the same muscle, but also that they have the same
innervation.   Indeed, in a few catfishes, e.g., *Chaca* (see
below), the palatine and more posterior section of the M.
adductor arcus palatini form a single continuous muscle.

These items of structural evidence regarding coordination
of maxillary movements in catfishes appear to lead to certain
operational problems (reduction of the oral cavity presumably
follows closely on raising of the mandible) that are un-
doubtedly more confusing to this author than to the catfishes.
Suffice it to say only that many if not all catfishes seem
able to move their maxillary barbels without noticeable dis-
location of their mouth structures, and that the development
of a separate palatine section of the M. adductor arcus
palatini is apparently the basis for doing so.

With regard to more mechanical matters, the autopalatine
may, as noted, slide over the lateral ethmoid flange, rock
around it, or both.   Judging from preserved specimens,
certain criteria of effectiveness determine to at least some
extent which type of autopalatine movement is adopted.   The
palatine part of the M. adductor arcus palatini normally
extends in a medial direction from the autopalatine to the
skull (fig. 1A-C).   Contraction of such a muscle will tend
to rock the autopalatine around the lateral ethmoid fulcrum,
and the autopalatine-maxillary hinge will be displaced
laterally.   Insofar as there is such a rocking motion, the
contraction of the M. adductor arcus palatini, the abutment
of the lateral ethmoid against the autopalatine, and the arc
of rotation of the maxillary and its barbel will all tend to
be in the same plane because "Muscles which act obliquely
generate useless forces at joints" (Alexander, 1965, p. 139).

The question perhaps arises of why a sliding motion of
the autopalatine over the lateral ethmoid flange is developed
by catfishes at all.   There seem to be two different mechani-
cal reasons for this.   One is exemplified by *Diplomystes*.
The maxillary of this fish swings through an almost vertical
arc.   To avoid the generation of useless forces at joints,
the fibers of the palatine part of the M. adductor arcus

palatini could theoretically be extended directly upward
and a rocking motion of the autopalatine adopted to accom-
plish maxillary extension. Actually *Diplomystes* has
developed a different mechanical system with an autopalatine
that slides and with a M. adductor arcus palatini that
extends almost directly backwards from the posterior end of
the autopalatine. Under such a system the palatine-maxil-
lary hinge is pulled directly back, and the arc of rotation
of the maxillary and its barbel would seem to be equally
effective in any plane (just as the spokes of an umbrella
open out equally effectively in various planes).

A different mechanical reason for a sliding autopalatine
seems to apply particularly to those forms with a very wide
arc of maxillary rotation. Examples are those catfishes
with very long maxillary barbels which are held back along
the sides (fig. 1A) when the fish is at rest, but which are
extended almost directly forward when the fish is hunting.
In such forms the maxillary extends into the base of the
barbel and hence, when the barbel is retracted, the
maxillary makes an acute angle with the autopalatine. If in
such fishes the anterior end of the palatine were displaced
laterally, the palatine-maxillary hinge would tend to close,
not open. It seems that to open such a hinge (fig. 1A) the
first movement of the autopalatine must be in a posterior
rather than a lateral direction (which necessitates a
sliding autopalatine-lateral ethmoid articulation), although
once the hinge opening becomes oblique, lateral movement of
the autopalatine head may be the more effective way of
swinging the maxillary anteriorly.

Forms in which the resting maxillary already extends out
at a relatively wide angle from the autopalatine, e.g.,
catfishes with the maxillary included in the gape, often are
restricted in the amount of sliding autopalatine movement.
This is probably most easily accomplished by reducing the
amount of flexibility in the membranous attachment between
the lateral ethmoid and the autopalatine. But many cat-
fishes go one or more steps beyond this, presumably for
mechanical reasons. If the extended or partly extended
maxillary meets any force from the front, this force will
push the distal part of the maxillary back and pull a sliding
autopalatine forward. If, however, the lateral ethmoid
flange extends into a secure socket in the side of the auto-
palatine (fig. 1B), forward sliding of the autopalatine will
be prevented. In short, forms with such blocks against
autopalatine sliding seem better able to force forward
maxillaries that form part of the upper border of the mouth,
e.g., many ground-feeding catfishes with subterminal mouths.
Indeed, in such fishes as *Synodontis* and many others (fig. 1B)
the forwardly moved maxillaries are used to pry the lateral
ends of the premaxillaries forward, thus approaching the
protrusile upper jaw of cyprinids.

Such a forcing system for the maxillaries is represented
in catfishes by several stages of development. The first of
these, already mentioned, is that in which a more or less

centrally notched autopalatine rocks around a lateral
ethmoid flange, like a teeter-totter. A further stage is
represented, in amphiliids for example, where the flange
projects forward behind a shelf on the autopalatine and a
more backwardly directed pull on the posterior part of the
autopalatine causes it to rock around the shelf (fig. 1C).
Such a system requires a firmer posterior abutment for the
lateral ethmoid flange than does the teeter-totter stage.
However, along this line of development the postarticular
part of the autopalatine may become progressively reduced
in size, as in loricariids.

THE PALATINE-MAXILLARY MECHANISM IN VARIOUS CATFISH GROUPS

In the palatine-maxillary mechanism, as in so many other
structures (see, for example, Regan, 1911; Alexander, 1965;
Chardon, 1968), *Diplomystes* stands apart from all other
living catfishes.
The distal part of the maxillary of *Diplomystes*, like
that of most cyprinids, characins, and other lower teleosts,
is expanded into a flat blade which projects down over the
side of the mandible. A flat, broad-based, tapering barbel
extends from the end of the maxillary. The teeth on the
maxillary of *Diplomystes* do not, as they do in characins,
extend directly downward, but rather down and in. Most of
the maxillary teeth, like those on the premaxillary and
dentary, are long, depressible, somewhat incurved, and flat-
tipped. The anterior (medial) end of the maxillary patch
has the teeth about three deep, the anteriormost of which
extend down and in from the lower rim of the maxillary.
There is a large, roundish patch of teeth on the vomer. The
vomerine teeth, like those elsewhere in the mouth, are
depressible and have flattened tips, but are shorter,
stouter, and more widely spaced than elsewhere.
Though the toothed maxillary of *Diplomystes* is certainly
primitive for catfishes, the depressible, flat-tipped teeth
on the maxillary and elsewhere provide a highly specialized
dentition. Also, *Diplomystes* is one of the relatively few
catfishes with larger teeth on the vomer than on the jaws.
This emphasis on vomerine teeth occurs again in the bagrid
Rita and in the Plotosidae and is presumably associated with
feeding specialization. By contrast, the usual siluroid
dentition is made up of bands of small, presumably grasping
teeth on various bones of the mouth roof, and when speciali-
zation occurs it is usually in the jaw teeth, with a reduc-
tion or total loss of dentition elsewhere.
Compared with the rodlike autopalatine of so many other
catfishes, that of *Diplomystes* has a rather complicated
shape. The anterior part has a horizontally expanded,
doughnutlike form with a hole passing vertically through it,
at least in the rather large (180 mm. S.L.) specimen examined.
The floor of the nasal cavity appears to extend down partway
into the hole. The part of the autopalatine anterior to the

hole is cartilaginous, and the anterior rim of the auto-
palatine is thus a transverse cartilaginous bar. The arti-
cular surface of the maxillary spreads broadly across the
front of this cartilaginous area in such a way as to form a
broad-based autopalatine-maxillary hinge that restricts the
swinging of the distal end of the maxillary to a single,
almost vertical plane. Behind the doughnutlike expansion,
the autopalatine slides under a lateral flange of the lateral
ethmoid. In the area under which the autopalatine passes,
the lateral ethmoid has a lateral projection from which
membranous tissue extends to an attachment on the outer sur-
face of the autopalatine. Judging from the preserved speci-
men, the membranous lateral ethmoid-autopalatine attachment
permits a certain amount of fore-and-aft sliding of the
autopalatine under the lateral ethmoid. The articular sur-
face between the autopalatine and the lateral ethmoid is
somewhat oblique, so that as the autopalatine moves backward
it is forced slightly downward. The autopalatine is entirely
free from the posterior part of the suspensorium. Behind
its sliding articulation it narrows to a strut that is
continued posteriorly as a long, tapering, cartilaginous
point (labeled *cc* by Alexander, 1965, fig. 4). The palatine
portion of the M. adductor arcus palatini inserts along the
cartilaginous extension and strut and extends almost
straight back to an origin on the skull.

When the palatine part of the M. adductor arcus palatini
contracts, the forward end of the autopalatine appears to be
displaced primarily backward, but also somewhat downward and
a little laterally. The effect in the preserved specimen is
to rock the distal end of the maxillary downward and forward.
The reason why the distal end of the maxillary swings forward
when its proximal end is pulled backward is not altogether
clear. I can find no particular ligamentous attachment bet-
ween the maxillary and the fixed premaxillary that might
serve as a fulcrum. Rather it seems that the membranous
tissue between the side of the lower jaw and the inner sur-
face of the mid-portion of the maxillary serves as the ful-
crum around which the maxillary rocks. If the proximal part
of the maxillary is pulled back with tweezers, the ligamen-
tous tissue from the mandible holds the central part of the
maxillary in place and its distal end rocks forward. But if,
in this specimen, the autopalatine is held in position and
the mandible is lowered, the distal end of the maxillary
again swings forward, presumably also because of the
mandible-maxillary ligamentous attachment.

I can find no adductor muscle for raising the lowered
maxillary and its barbel; however, raising the lowered
mandible brings this about in the preserved specimen. Thus,
so far as can be determined from a preserved specimen, it
appears that in *Diplomystes* the palatine-maxillary mechanism
serves as an additional system to mandibular lowering for
swinging the distal end of the maxillary and its barbel
downward and forward, but that retraction of the lowered
maxillary is dependent on raising the mandible.

At first sight, the rather complicated shape of the autopalatine of *Diplomystes* seems specialized. However, this shape, as already noted, shows considerable resemblance to certain autopalatine types in cyprinids and cobitids. The question of primitiveness versus specialization in the *Diplomystes* palatine, therefore seems best left unanswered.

Unlike the situation in many catfishes, there is, at least in the specimen of *Diplomystes* dissected, no mesopterygoid link between the autopalatine and the posterior part of the suspensorium. Indeed, I can find no separate mesopterygoid of any sort, either in the area labeled *ms* in Alexander's (1965) figure 4 or elsewhere, though Lundberg (*in litt.*) reports a mesopterygoid in cleared and stained specimens. The posterior part of the suspensorium of *Diplomystes* is peculiar in several respects. The hyomandibular articulation with the skull is unusually long, as Alexander (1965) has noted. The metapterygoid has two well-developed anterior prongs. One extends medially below the cranial nerves. The other passes forward ventrolaterally to beside the autopalatine; the anterior end of this prong provides an origin for a ligament attached anteriorly to the side of the vomerine plate (and is hence reminiscent of the condition in the bagrid genus *Rita*).

The question arises of why *Diplomystes* alone among living catfishes has retained a toothed maxillary of generalized lower teleostean type. A partial answer to this lies, I think, in certain differences between the bottom-feeding adaptations of *Diplomystes* and those of other siluroids. In other catfishes the maxillary is part of a complex barbel apparatus that moves more or less independently of the jaws. In *Diplomystes* the maxillary remains part of the jaw apparatus, and certain nonbarbelled sensory specializations have been developed which are apparently used in combination with the maxillary barbel in locating food. In *Diplomystes* tremendous cranial nerve rami pass forward into the fleshy upper lip, which is directed downward in front of the mouth. Similar rami, less extensively developed, occur in certain other catfishes, e.g., *Trichomycterus*. Alexander (1965, p. 97) has stated regarding *Diplomystes*: "A very large foramen, between parasphenoid, pterosphenoid and prootic, corresponding to the sphenoid fissure of the chondrocranium, must have given passage to the optic, trigeminal and facial nerves. In all other catfish, the parasphenoid and pterosphenoid meet immediately posterior to the optic nerve." In *Diplomystes* the large nerve rami to the upper lip issue from this foramen, and its enlargement seems to be to accomodate them. I assume that these rami are associated with taste perception in the upper lip. If this is correct, it seems to follow that the upper lip is closely applied to the bottom during feeding. Certain other structural features in *Diplomystes* are in accord with such an assumption. The dentition is of a specialized, perhaps scraping type. *Diplomystes*, unlike most catfishes, has no mental (or nasal) barbels. Instead, the lateral line pores on the chin open

from small hummocks in clearly distinguished bare areas.
Finally, forward movement of the maxillary carries its bar-
bel downward and forward to below the chin as in cyprinids,
not more or less laterally as in other catfishes where
mental barbels perhaps serve as bottom probes.

If the maxillary part of the palatine-maxillary mechanism
of *Diplomystes* represents a more primitive stage of struc-
tural evolution than that of other catfishes, the palatine
part of the same mechanism in certain other catfishes seems
to be more generalized than that of *Diplomystes*. In
cyprinids and cobitids the anterior end of the mesopterygoid
has a membranous attachment to the under surface of the
skull and, more laterally, a movable articulation with the
posterior end of the autopalatine. In a number of catfish
families a rather similar mesopterygoid arrangement occurs,
and in such families the mesopterygoid seems to retain its
function, considerably modified, of a movable link between
the autopalatine and the posterior part of the suspensorium.
The most general level of palatine-maxillary organization,
other than that of *Diplomystes*, is here considered to be
that in which the mesopterygoid forms such a link. Among
catfishes with this type of mesopterygoid, the greatest
variability in palatine-maxillary mechanisms is found in the
Bagridae, which will be discussed first. Indeed, it seems
possible, so far as structural change is concerned, to trace
all of the types of catfish palatine-maxillary mechanism
except that of *Diplomystes* and perhaps of the Amblycipitidae
to one or another of the forms of this structural complex
found in the Bagridae.

Variation in bagrid suspensorial structure was used as
a basis for classifying genera by Regan (1911). His first
character for distinguishing his two subfamilies Bagrinae
and Chrysichthyinae is a difference in mesopterygoid-
pterygoid relationship. In the bagrids I have examined I
have not been able to follow the distinction Regan makes,
nor have I seen any bagrid that corresponds at all well with
the figure (1B) Regan gives for the suspensorium of *Clarotes*,
a genus unavailable to me. The great variability in bagrid
suspensorial structure, even within a single genus (*Mystus*),
is illustrated by Tilak (1965b). Jayaram (1966) recognizes
five bagrid subfamilies. A member of each of these five
subfamilies was dissected. These five species, together
with material from other bagrids examined, are discussed
below (table 1).

In all of the bagrids examined except *Rita* a mesoptery-
goid is movably associated with the autopalatine laterally
and, by ligament, with the metapterygoid posterior to it.
Insofar as the nature of this mesopterygoid link can be
shown on a flat surface, it is well illustrated in Starks'
(1926, p. 178) figure of the ariid *Felichthys*. The medial
end of the mesopterygoid is ligamentously attached to the
skull anteriorly and to the metapterygoid posteriorly. The
mesopterygoid extends distally to below the posterior end
of the autopalatine. Here, it usually has an anteriorly-

directed projection which extends forward below the auto-palatine, to which it is membranously attached.   In most bagrids the mesopterygoid is a single structure of complex shape, but in *Bagroides*, as in ariids (Starks, 1926, fig. 11), it consists of two separate ossifications, one extending from the skull to the autopalatine, and the other a small ossicle firmly lodged on the lower surface of the auto-palatine.

In *Rita*, unlike the other bagrids I have examined, there is no mesopterygoid association with the autopalatine. Hashmi (1957) and Jayaram (1966, fig. 1, msp) have recorded a mesopterygoid in this genus, but the only bone I have found that might be identified as such seems to me to be more probably a fragmented part of the metapterygoid (see above).   *Rita*, like *Diplomystes*, has a vomerine tooth plate expanded into the area in which a mesopterygoid-autopalatine link would ordinarily occur.   The dissociation between the mesopterygoid and the autopalatine may also be represented in *Clarotes* (Regan, 1911, fig. 1B), a bagrid genus I have not seen, and certainly occurs in a whole series of more advanced catfish types (see below).

In bagrids the maxillary is sometimes included in the upper lip, i.e., it forms part of the upper border of the gape, and sometimes the upper lip extends up as a separate structure to below the maxillary base so that maxillary movement is independent of changes in the shape of the mouth opening.

The two bagrid genera examined in which the maxillary is included in the gape (*Chrysichthys* and *Auchenoglanis*) have certain other palatine-maxillary characteristics in common. In the first place, their maxillaries are larger than those of other bagrids (Jayaram, 1966).   In the second, their autopalatines rotate around a protruding cartilaginous-tipped articular facet on the lateral face of the lateral ethmoid which blocks any sliding of the autopalatine.   In certain other respects, however, the palatine-maxillary mechanisms of these two genera differ greatly from one another.   At least some of these differences seem to be associated with the fact that *Chrysichthys* is round-headed whereas *Auchenoglanis* is flat-headed.   Thus, the maxillary of *Chrysichthys* extends back over a somewhat arched gape.   For-ward rotation of its distal end and barbel are consequently through a ventrolateral arc.   Also, the articular facet on the lateral ethmoid is more ventrolaterally directed and the M. adductor arcus palatini pulls dorsomedially.   In *Auchenoglanis* the maxillary extends laterally over the flat gape, the articular facet of the lateral ethmoid is laterally directed, and the M. adductor arcus palatini pulls backward. The main difference in the palatine-maxillary mechanism of *Chrysichthys* and *Auchenoglanis*, however, is that in *Chrysichthys*, as in most catfishes, the resting maxillary and its barbel are held back along the body and the main muscular effort seems to be exerted in the extension of these structures, whereas in *Auchenoglanis* the maxillary is

held out at an angle to the body and the principal muscula-
ture seems to cause its retraction. The maxillary barbel
structure appears to be associated with the small amount of
maxillary extension in this fish; the barbel is thick-set
with musculature entering its base which extends out at an
angle to the maxillary bone. That this barbel can be moved
forward separately from the maxillary bone is demonstrated
by the position of the barbel in Sterba's (1959, fig. 494)
photograph of the living fish. This relationship between
the barbel and the maxillary bone of *Auchenoglanis* is
paralleled in such other catfishes as *Chaca* and *Plotosus*.

So long as the maxillary is included in the gape, its
arc of movement is limited by the upper lip, but once the
maxillary becomes free of the gape, the potential arc of
movement is much wider. For example, in *Mystus* the maxillary
extends into the base of a long, relatively stiff barbel that
can apparently be swung through an arc of nearly 180 degrees.
Other fishes with this type of barbel, and presumably *Mystus*,
normally hold the barbel back along the sides but extend it
almost directly forward when hunting. As already discussed,
this type of barbel apparently requires an autopalatine that
can be moved in an anteroposterior direction, i.e., one
that slides over the lateral ethmoid flange. In *Mystus*,
Bagroides, and apparently to some extent in *Rita* (the bagrids
investigated in which the maxillary is more or less excluded
from the gape) the rodlike palatine appears to be capable of
some sliding movement. That retraction of the autopalatine
also results in some rocking around, as well as sliding over,
the lateral ethmoid flange seems to be indicated by the M.
adductor arcus palatini, which extends medially into its
origin on the skull.

There are a number of catfish families in addition to
the Bagridae in which at least some members have a mesoptery-
goid link between the autopalatine and the posterior part of
the suspensorium. This link is usually, as in bagrids,
between the autopalatine and the metapterygoid. But in the
amblycipitids *Liobagrus* (Regan, 1911, fig. 1C) and *Amblyceps*
(Tilak, 1967a, fig. 2) the mesopterygoid seems to have the
usual anteromedial ligamentous attachment to the skull as in
bagrids and has a lateral prong extending under the auto-
palatine, but instead of a ligamentous connection between
the mesopterygoid and the metapterygoid, the mesopterygoid
has a long extension passing back alongside the small
metapterygoid nearly to the hyomandibular. The only remote
resemblance to this amblycipitid mesopterygoid that I know
of in other catfishes is the bone labeled *AB* in Tilak's
(1963a) figure 42 of the sisorid *Glyptosternum* and this bone
has a projection extending forward, not backward, from the
lateral arm.

Certain Old World catfish families have at least some
members that resemble such bagrids as *Mystus* not only in
having a mesopterygoid ligamentously attached posteriorly to
the metapterygoid and extending laterally to just below the
autopalatine, but also in having a rodlike sliding auto-

palatine and the maxillary excluded from the gape.   Such
families include the Pangasiidae (Tilak, 1964a, figs. 7, 8)
and the Schilbeidae (*Schilbe* examined).
     The semimarine circumtropical family Ariidae also has
most of the characteristics mentioned above but is closer to
Bagroides than to *Mystus* in having the mesopterygoid repre-
sented by two separate parts, the anterior of which is
firmly attached to the under side of the autopalatine
(Starks, 1926, fig. 11; Tilak, 1965a).
     In the South American family Doradidae, *Trachelyopterus*
has all of the palatine-maxillary features of *Mystus* listed
above.   However, other members of the family, such as *Hassar*,
have subterminal mouths with the maxillaries included in the
gape, though they retain the long barlike sliding auto-
palatine.
     The mesopterygoid condition in the South American family
Pimelodidae appears to be more varied.   In *Pimelodus* the
mesopterygoid is a long curved, wirelike bone that has the
usual basal ligamentous attachment to the skull; it extends
around the palatine portion of the M. adductor arcus
palatini to below the autopalatine.   Regan (1911) records an
apparently similar mesopterygoid (under the name pterygoid)
from the pimelodid genera *Callophysus* and *Sciades*, as well
as from *Pimelodus*.   In *Pseudopimelodus* the mesopterygoid is
not a wirelike ossicle extending around the back of the
palatine part of the M. adductor arcus palatini but rather
a broad, flat plate extending laterally below this muscle;
its distal rim is just below and membranously attached to
the autopalatine.   In *Rhamdia* the mesopterygoid, as in
Pseudopimelodus, is a flattened plate extending laterally,
but its distal rim is well below and completely separated
from the autopalatine.   Thus, there is a transition within
the Pimelodidae from types of mesopterygoid in *Pimelodus* and
Pseudopimelodus, essentially similar to those in the Bagridae,
to a condition in *Rhamdia* which closely approaches that of
the mesopterygoids of such families as the Ictaluridae,
Plotosidae, and Siluridae.   This transition is accompanied
by certain changes in palatine-maxillary musculature.   In
Rhamdia there is a well-developed M. retractor tentaculi
originating on the metapterygoid and inserting on the poste-
rior surface of the maxillary lateral to the palatine-
maxillary hinge; the metapterygoid apparently serves as a
fixed point toward which contraction of this muscle pulls
the distal end of the maxillary.   In *Pimelodus* there is no
M. retractor tentaculi.   Instead there are two ligaments
inserting on the maxillary lateral to the palatine-maxillary
hinge.   The more lateral of the two originates on the
coronoid process of the mandible; it appears to be slack
except when the mouth is almost completely or completely
closed.   The medial of the two ligaments extends back to an
origin on a point of bone projecting laterally from the
metapterygoid.   In *Pimelodus* the retraction in part, like
the extension of the long maxillary barbel, appears to be
coordinated with movement of the posterior part of the

suspensorium. *Pseudopimelodus* has the same two ligaments
extending from the maxillary as does *Pimelodus*, but the
medial of the two extends farther posteriorly than in
Pimelodus.

Another South American family in which a mesopterygoid
link, but of a different type, appears to be present between
the autopalatine and the metapterygoid is the Trichomycteri-
dae.   In *Nematogenys* the autopalatine, mesopterygoid, and
metapterygoid are all on the same plane, with flat surfaces
just above the fleshy roof of the mouth.   The mesopterygoid
is a small plate of bone between the posterior end of the
autopalatine lateral to it, the skull medial to it, and the
metapterygoid posteriorly.   The autopalatine in *Nematogenys*,
as in all of the trichomycterid series of families, has a
firm posteromedial abutment against the lateral ethmoid
flange (not shown in Regan's, 1911, fig. 2).   In *Tricho-
mycterus* the general configuration of the palatine-maxillary
mechanism is about as in *Nematogenys*, but the mesopterygoid
is absent.

Chardon (1967, 1968) has established the relationship
between the South American families Trichomycteridae,
Aspredinidae, Callichthyidae, Astroblepidae, and Loricariidae.
Aside from the Trichomycteridae, the only family in the
group from which a mesopterygoid has been reported is the
Aspredinidae.   Regan (1911, p. 575) says: "...mesopterygoid,
when present, small, attached to the lateral ethmoid."   No
mention is made of which aspredinids have mesopterygoids.
I have dissected a specimen of *Aspredinichthys filamentosus*.
In this specimen there is a band of ligamentous tissue
extending forward from the quadrate.   In this band is a
bone free at both ends from other ossifications.   I interpret
this bone as a metapterygoid, not a mesopterygoid; if it is
a mesopterygoid, then there is no metapterygoid.   The sheath
in which it is embedded continues forward and divides into
two parts.   The larger upper part is attached to the lower
surface of the autopalatine and the smaller lower part to
the outer end of the movable premaxillary.

For geographic reasons and because of certain superficial
similarities between some members of the trichomycterid-
aspredinid-callichthyid-astroblepid-loricariid series and
Diplomystes, the possibility that the series evolved from a
Diplomystes-like ancestor and not from the bagrid stock was
considered and explored.   The palatine-maxillary mechanism
does not support such a possibility.   However, the palatine-
maxillary mechanisms of *Nematogenys*, *Aspredinichthys*, and
other members of the series appear to have evolved in a way
that is not closely paralleled in other catfishes I have
investigated.

With regard to the Chacidae Regan (1911, p. 457) states:
"...the small mesopterygoid is attached to the lower surface
of the palatine."   Again I have not been able to find this
bone, this time perhaps because of the small size of the
specimen of *Chaca* dissected (78 mm.).   In this specimen the
metapterygoid extends forward as a flat plate under the

autopalatine (about as indicated in Regan's 1911, fig. 2D). From the upper surface of the anterior part of the metaptery-goid a short, strong ligament passes upward to the under surface of the autopalatine. The palatine and posterior parts of the M. adductor arcus palatini in *Chaca* form a single continuous sheath of musculature passing medially to an origin on the skull.

In the rest of the catfishes to be considered the meso-pterygoid is not associated with the autopalatine; it is either a platelike bone more or less closely attached to the front of the metapterygoid or it is absent. In most of the families to be mentioned the lateral ethmoid flange extends into a more or less well-developed socket on the autopala-tine which restricts or prevents sliding of the autopalatine. The exception is the family Plotosidae.

In the Plotosidae the mesopterygoid is a small platelike bone attached to the skull anteriorly and to the metaptery-goid posteriorly. The autopalatine is a long rod the move-ment of which is blocked posteriorly by a semicircular ridge rising from the upper surface of the metapterygoid. The M. adductor arcus palatini extends anteromedially from the back of the autopalatine to the skull. The maxillary is a rather large bone included in the gape, and the maxillary barbel extends out at an angle from the long axis of the maxillary. From manipulation of preserved specimens it appears that contraction of the M. adductor arcus palatini pulls the autopalatine forward, rather than backward as in other cat-fishes. Since the movable premaxillaries of *Plotosus* extend laterally in front of the maxillaries, it seems that forward movement of the autopalatine and palatine-maxillary hinge has the effect of forcing the distal parts of the premaxil-laries forward and downward and of rotating the large pre-maxillary teeth forward. Other catfishes use autopalatine movement as a means of moving the premaxillaries, but they do not do so by pulling the autopalatine forward. The reversal of usual maxillary movement seems to be reflected not only in the position of the maxillary barbels but in the maxillary retractor mechanism. This consists of ligamentous tissue extending from the back of the maxillary to the outer surface of the M. adductor mandibulae. Takahasi (1925) pointed out that this arrangement resembles the retractor system for the maxillary in cyprinids, which he considers a maxillary component of the M. adductor mandibulae. Because of this similarity between *Plotosus* and cyprinids Takahasi postulated an origin of the M. retractor tentaculi of cat-fishes in the maxillary part of the M. adductor mandibulae of cyprinids and other teleosts. Perhaps so, but the retractor system for the maxillary of *Plotosus* is a special case; in other catfishes with a M. retractor tentaculi, this muscle extends deep to and is separate from the M. adductor mandibulae (McMurrich, 1884).

The family Ictaluridae has usually been placed with the Bagridae and Pimelodidae, as by Regan (1911). In general appearance the palatine-maxillary mechanism of ictalurids

supports such a placement, but the mechanism differs in particular features from that of either family. The plate-like mesopterygoid ahead of the metapterygoid and separate from the autopalatine in ictalurids is essentially of the type found in such pimelodids as *Rhamdia*. The differenti-ation of this type of mesopterygoid from that usually found in bagrids has occurred within the Pimelodidae (see above) and may have evolved repeatedly, for it is present in a number of catfish families. The maxillary of ictalurids, unlike that of pimelodids, is included in the gape as in the bagrids *Chrysichthys* and *Auchenoglanis*, and, as in those two genera, the lateral ethmoid flange of ictalurids extends into a rounded socket on the autopalatine.

In its major features the palatine-maxillary mechanism of *Clarias* is essentially similar to that of ictalurids. Certain differences are probably associated with the flat-headedness of *Clarias*. In such fishes there seems to be a tendency to move the corners of the mouth anteriorly so that the arched gape of high-headed forms becomes transverse in flat-headed catfishes. Such a change is often accompanied by enlargement of the laterally extended maxillary, as in *Auchenoglanis* and *Chaca*. In *Clarias* this development seems to have been carried a step farther by incorporating the corner of the mouth into the laterally extending maxillary barbel, for the lower lip is attached laterally to the lower surface of the barbel.

The Sisoridae and Amphiliidae are primarily hill-stream catfishes of Africa and Asia respectively. As might be expected, both have subterminal mouths with the maxillaries included in the gape. However, the palatine part of the palatine-maxillary mechanism is quite different in the two families. In the Sisoridae (Tilak, 1963a; Mahajan, 1966), as in the Clariidae (Burne, 1909, p. 624, fig. 196A) and to a lesser extent in the Ictaluridae, the autopalatine is a rodlike structure which rocks around a barlike extension of the lateral ethmoid in teeter-totter fashion (fig. 1B). This type of autopalatine mechanism appears to be fore-shadowed in the Asiatic bagrid genus *Leiocassis*, which has an essentially similar autopalatine-lateral ethmoid arti-culation. In the African Amphiliidae (Harry, 1953), as in the Malapteruridae (Burne, 1909, p. 629, fig. 197) and Mochokidae (see below), the autopalatine has at most a short, tapering projection behind the lateral ethmoid articulation (fig. 1C). This autopalatine type is essentially that of the African bagrid genera *Chrysichthys* and *Auchenoglanis*.

The Mochokidae and Siluridae are the only other families that will be mentioned. Both of these families have highly specialized palatine-maxillary mechanisms and both include forms in which the palatine has moved entirely to the front of the lateral ethmoid flange (as in fig. 1D). In other respects the palatine-maxillary mechanisms of the two families are wholly different. In *Silurus* (Jobert, 1872), the maxillary rocks around a ligamentous attachment to the firmly fixed premaxillaries (as in fig. 1A), and there is a

sliding articulation between the short, nodular palatine and the ethmoid region of the skull. In the Mochokidae, the palatine rocks around the ethmoid flange and maxillary extension moves the premaxillary forward (fig. 1C). Also, in at least the mochokids *Euchiliichthys* (fig. 1D) and *Synodontis* there is a maxillary extensor muscle between the anterior tip of the palatine and the front surface of the maxillary that I have not noted elsewhere in catfishes.

Conclusions Regarding the Palatine-Maxillary Mechanism

Only the basic features of the evolution of the palatine-maxillary mechanism in modern catfishes will be discussed here.

A toothed, distally expanded maxillary and a mesoptery-goid link between the autopalatine and the posterior part of the suspensorium have been postulated as characters of certain modern catfishes that have been inherited from an ancestral siluroid stock. These two characteristics do not occur in any one catfish today. *Diplomystes* is the only modern form with a toothed maxillary. It also has a number of other characteristics, some presumably primitive and others apparently specialized, that do not occur in other siluroids. *Diplomystes* is therefore considered as a relict form well separated from the main stem of catfish evolution.

A mesopterygoid link between the autopalatine and the posterior part of the suspensorium occurs in a number of catfish families. It appears in two basal forms. One is represented only in the Amblycipitidae, in which the meso-pterygoid passes back alongside the small metapterygoid to or almost to the hyomandibular. This type of link may represent a specialization from the form that occurs else-where, but it may be a separate development. In all other catfishes with a mesopterygoid, that bone is attached by ligament or directly to the anterior end of the metaptery-goid.

Of the modern catfish families with a mesopterygoid link present between the autopalatine and the metapterygoid, the Bagridae shows the greatest palatine-maxillary variation. This variation is divisible into three basic categories. In one, represented only by *Rita*, expansion of the vomerine tooth plate appears to have led to the loss of the meso-pterygoid link (a similar loss for a perhaps similar reason has occurred in *Diplomystes*).

A second type of bagrid palatine-maxillary structure occurs in all of the Asiatic bagrids I have examined (except *Rita*) and in the African *Porcus* (or *Bagrus*). Here, the maxillary is free from the gape and the autopalatine is a rod-shaped bone that usually slides over the lateral ethmoid flange. Other families with a sliding autopalatine in which at least some members have the maxillary free from the gape and a mesopterygoid link between the autopalatine and the metapterygoid are the Pimelodidae, Doradidae, Ariidae,

Schilbeidae, and Pangasiidae. This group of families, to-
gether with the Bagridae, contains to my knowledge all those
catfishes with the maxillary extending into a long, rela-
tively stiff barbel that can be rotated through an arc of
nearly 180 degrees. So far as change from ancestral teleosts
is concerned this barbel type represents about the greatest
differentiation that occurs in catfishes. Yet it is present
in a group of families placed (*Diplomystes* aside) at the
base of the modern siluroid series, whatever point of view
is considered. There seems no reason to believe that the
type of palatine-maxillary mechanism represented in these
families has been developed more than once.

The other main type of palatine-maxillary mechanism in
bagrids is that of the African genera *Chrysichthys* and
Auchenoglanis. In these the mesopterygoid link is present
as usual in bagrids, the maxillary is included in the gape,
and the autopalatine is propped more or less securely
against the lateral ethmoid in a socketed articulation. A
rocking articulation of a different type seems to be in the
process of development in the Asiatic bagrid *Leiocassis*, and
one of still another sort is present in the South American
trichomycterid series of catfishes. It seems clear that a
rocking autopalatine articulation has developed a number of
times in catfishes and that, at least in *Leiocassis*, this
development can be traced back to forms with sliding auto-
palatines of the *Bagrus* type. Though the source of the
trichomycterid palatine-maxillary mechanism is not clear, at
least to me, there seems no reason to believe that it, or
the palatine-maxillary mechanism of any other modern catfish,
has evolved directly from that of *Diplomystes*.

Evolution and Zoogeography of Modern Siluroids

In this section the palatine-maxillary mechanism will be
used as a primary basis for suggesting some working hypo-
theses concerning the evolution and zoogeography of modern
catfish groups.

Within the ostariophysine fishes, which are undoubtedly
of monophyletic origin, it is generally agreed that the
earliest split is that between the catfishes on the one hand
and the characins, gymnotids, cyprinids, and their allies on
the other. The differences in distribution patterns between
these two major divisions (Siluroidei and Cyprinoidei) have
been the subject of considerable discussion, most recently
by Gosline (1975). Because of a possible relevance to what
will be said below, the distribution of the Cyprinoidei will
be briefly stated. The gymnotoid families are restricted to
South America (with the exception of certain extensions into
Central America). The characins occur today in South (and
Central) America and Africa, though fossil characin teeth
have been recently recorded from France (Cappetta, *et al.*,
1975). The cyprinids and their allies are most diversified
in eastern Asia, but also occur in Europe, North and Middle

America, and Africa.

Unlike the Cyprinoidei, the Siluroidei is not divisible into diversified, distinct sections. Rather, the main division lies between *Diplomystes*, a relict South American genus, on the one hand and all the rest of the siluroids on the other. The question arises of how to divide the non-*Diplomystes* catfishes for purposes of further analysis. The following discussion adopts one possible basis (for a very different one, see Chardon, 1968).

For reasons that have been discussed in the body of the paper, those catfishes with a mesopterygoid link between the metapterygoid and a bar-shaped, sliding palatine, the maxillary usually free from the lip, and often with long, stiff maxillary barbels will be considered closest to the basic stock of modern siluroids so far as palatine-maxillary structure is concerned. Families in which at least some members have these characteristics are: Ariidae, Doradidae, Pimelodidae, Bagridae, Schilbeidae, and Pangasiidae. The Schilbeidae and Pangasiidae are generally thought to be bagrid derivatives, e.g., by Chardon (1968), and will not be considered further. Of the other families, the Ariidae is circumtropical with mostly marine and estuarine forms; the rest are almost completely freshwater catfish groups. The doradids and pimelodids are restricted to South and Central America, and the bagrids are found in Asia and Africa. All of the families mentioned above contain fishes that live primarily in large, unobstructed waters.

Gosline (1973) on anatomical grounds suggested that the ostariophysine fishes originated as small, upland stream forms, but that the catfishes may have become the first of the ostariophysines to have developed large-river and thence estuarine types (Gosline, 1975; see also Rossi, 1951). If the above hypotheses are correct, a relatively early catfish dispersal across lowland and/or marine barriers impassable at that time to the Cyprinoidei may in part explain why the basal pimelodid-bagrid group of catfishes is represented today from South America through Asia whereas none of the groups of the Cyprinoidei have so wide an intercontinental range. In any event, the siluroids are the only ostario-physine group that has developed fully adapted and well-differentiated marine families (Ariidae and Plotosidae).

To return to the ariid-doradid-pimelodid-bagrid series, the Ariidae not only is a family of circumtropical dis-tribution made up mostly of marine or semi-marine forms, but is recorded as far back in the fossil record (Eocene) as any catfish family. Nevertheless, in a number of char-acters outside the palatine-maxillary system the ariids are highly specialized. Thus, ariids are the only catfishes other than doradids with long backward extensions of the epiotics (see, for example, Chardon, 1968). It therefore seems highly improbable that any catfish group, other than perhaps the Doradidae, has been derived from the Ariidae.

So far as relationships are concerned, the Doradidae is an enigmatic family with some specialized characters held

in common with the ariids (but perhaps developed indepen-
dently) and other features that suggest a pimelodid deri-
vation.

The two basal groups that remain to be discussed are
the South American pimelodids and the Old World bagrids.
Though the palatine-maxillary data provide weak supporting
evidence at best, they in no way contradict Regan's (1911)
view that the various South American catfish families other
than the Diplomystidae, Ariidae, and Doradidae have been
derived from the Pimelodidae.

In the Old World the palatine-maxillary data suggest
that the Bagridae is divisible into two primary groups: a
basal Bagrinae that includes all of the Asiatic forms plus
the single African genus *Bagrus* (or *Porcus*), and a deriv-
ative African Chrysichthyinae. The Chrysichthyinae could
well have given rise to the African endemic families
Mochokidae, Amphiliidae, and Malapteruridae so far as pala-
tine-maxillary structures are concerned. The Bagrinae, in
regard to these same structures, could have provided the
base not only for the Eurasian catfish families, except
possibly the Amblycipitidae, but for the North American
Ictaluridae as well.

If these conclusions concerning catfish evolution are
correct, they give rise to the zoogeographic difficulty of
having two primary centers of catfish diversification (South-
east Asia and South America) separated by a continent (Africa)
that is a secondary center of catfish evolution. The fact
that the Cyprinoidei can well be interpreted as having the
same two primary centers of diversification (see, for
example, Banarescu, 1971) does nothing to remove the incon-
venience of Africa's geographic position for such interpre-
tations.

It seems well to stress once again the provisional nature
of the working hypotheses presented in this discussion. The
zoogeographical problem of Africa raised in the last para-
graph, for example, may well turn out to be a 'pseudo-
problem.' If it really exists, it was already solved in
pre-Eocene times because, as Regan (1922) pointed out, the
present intercontinental distribution of the major ostario-
physine groups was already pretty well established in the
Eocene.

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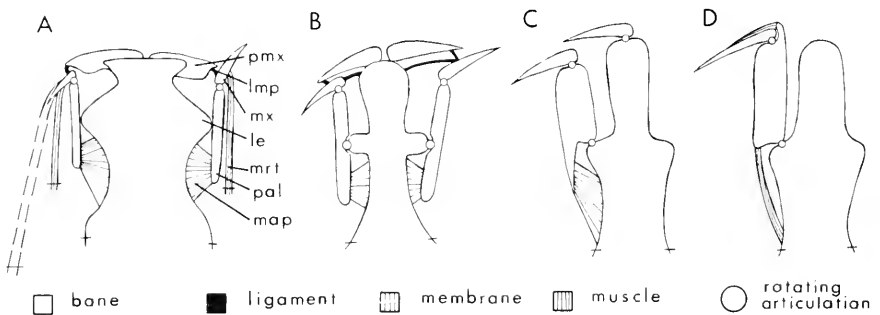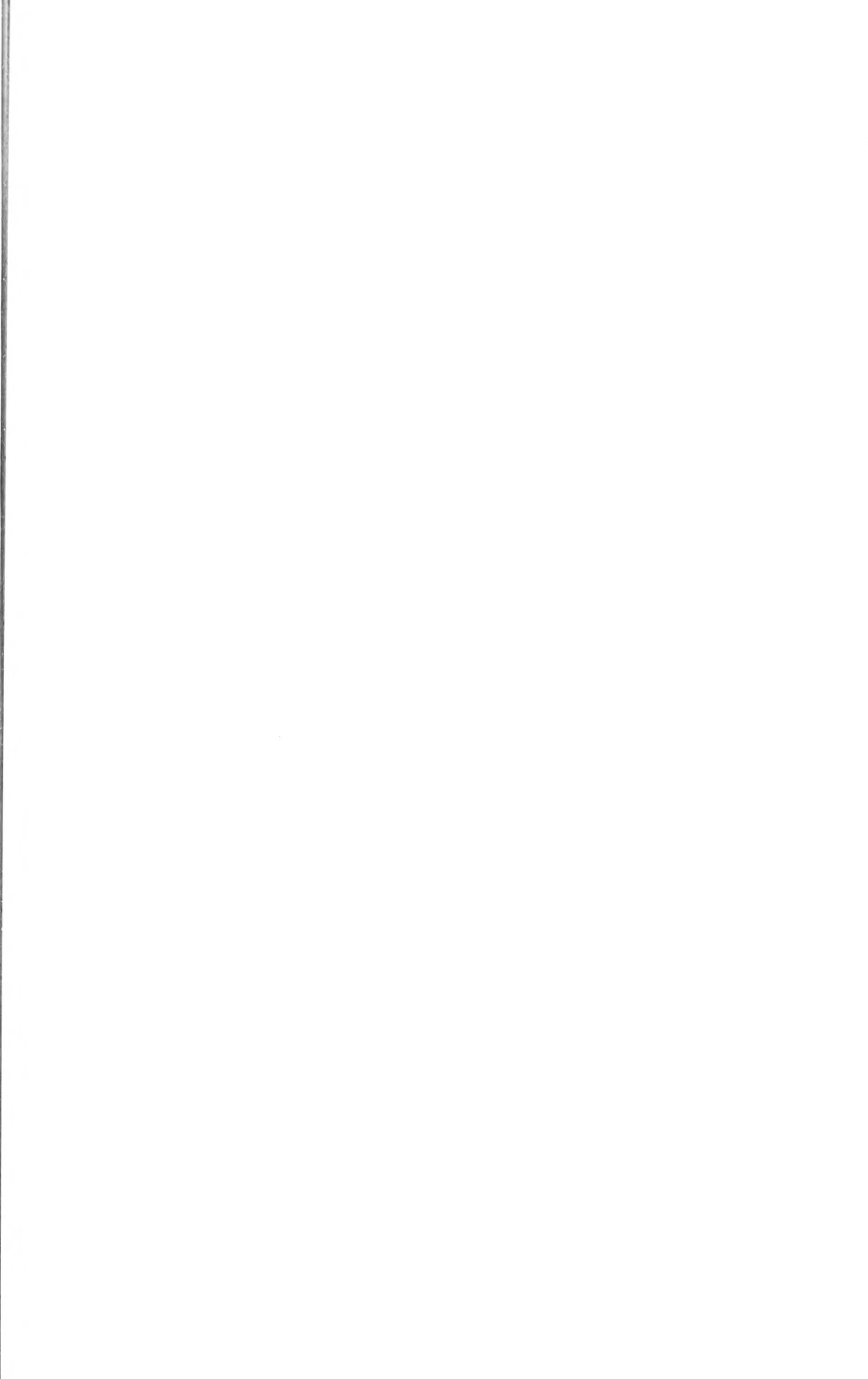   110, 30 figs.

FIGURE 1.   Diagrammatic representation of different
types of palatine-maxillary mechanisms in catfishes (dis-
cussed in text).   The paired dashed line on the left side of
A indicates the maxillary barbel, which is not shown else-
where.   A: sliding type of palatine-skull articulation;
B-D: different types of rocking articulations.   In A the
premaxillary is firmly united to the skull and the maxillary
rocks around the maxillary-premaxillary ligament; in B and C
the premaxillary is membranously attached to the skull and
its lateral end moves with the maxillary.   In A and B the
retracted condition of the maxillary (with its barbel) is
shown on the left side and the extended condition on the
right.   In D the premaxillary is not indicated.   le, Lateral
ethmoid; lmp, maxillary-premaxillary ligament; map, M.
adductor arcus palatini; mrt, M. retractor tentaculi; mx,
maxillary; pal, autopalatine; and pmx, premaxillary.

TABLE 1. *Characteristics associated with the palatine-maxillary mechanism in bagrids dissected.*

	Ritinae	Chrysichthyinae	Bagrinae	Bagroidinae	Auchenoglanidinae
	Rita rita	*Chrysichthys auratus*	*Mystus nemurus*	*Bagroides melapterus*	*Auchenoglanis ballayi*
Head shape (in cross section)	rounded	rounded	flattened	rounded	flattened
Maxillary in relation to upper lip	largely excluded	included	excluded	excluded	included
Relative size of maxillary	small	moderate	small	small	large
Palatine articulation with lateral ethmoid	sliding to some extent	lateral ethmoid projects into a socket on the autopalatine	sliding	sliding	autopalatine socketed
Palatine position relative to the lateral ethmoid	ventrolateral	lateral; ventro-lateral in some other species of *Chrysichthys*	lateral	ventral	lateral
Direction of pull of the palatine part of the M. adductor arcus palatini	dorsomedial	dorsomedial	posteromedial	postero-dorso-medial	straight back
Mesopterygoid	absent	hooked under autopalatine	with a long forward prong under the autopalatine	in two parts, the posterior an ossicle under autopalatine	hooked under autopalatine
Metapterygoid	suturally united to hyomendibular and quadrate	with a cartilaginous flexible junction with quadrate	suturally united to quadrate	suturally united to hyomandibular and quadrate	united to quadrate